



A comparison of modelled and measured millet production in northeastern Burkina Faso

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Abstract

Millet production has been monitored in the northern part of the Sahelian zone at the village Petakole located near Dori, NE Burkina Faso. Different methods, ranging from interviewing the local farmers to eddy covariance measurements of CO_2 -fluxes, have been applied for estimating the total biomass and grain yield. Using field measurements conducted in 1997, a mechanistic photosynthesis model was calibrated to suit the current, local environment. A comparison of the daily net assimilation measured by the eddy covariance method and modelled by the photosynthesis model shows that more than 85% of the day-to-day variation in assimilation can be described by the model. An analysis of the diurnal variation in CO_2 -fluxes over the growing season reveals that midday radiation load and leaf temperature are the most important climatic-hydrological parameters for predicting the carbon assimilation. At the end of the growing season when the soil moisture content is low (<8 vol.%) the rate of carbon assimilation is also limited by the stomatal control. For 1996 and 1997 the total CO_2 -uptake is compared to millet yield estimates (in $kg\ m^{-2}$) obtained through interviews with the local farmers and using

aerial photos and GPS for determining the field sizes. The estimated millet yields are found to be much higher for 1997 than for 1996 and in both years with a 25% difference between the two yield estimation methods.

Keywords

Photosynthesis, millet, CO_2 -modelling, grain yield.

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The Sahelian landscape and its vegetation differ in a number of ways from what is found in most parts of the industrialized world. Both the natural and cultivated vegetation found in this landscape are much more sparse than what is found in the temperate part of the world, and because irrigation and artificial fertilization only play a minor role, the harvest depends much more on the natural environment. In the Sahel, the climate in particular fluctuates strongly (Nicholson, 1994; Thornton et al., 1997). The coefficient of variation in annual rainfall is high (22% over the last 30 years within the study area of Dori, Burkina Faso) and this fact combined with the low annual rainfall of 400-600 mm creates high risk of crop failure and famine. Much recent research has focused on early warning of famine (Thornton et al., 1997) and on methods that enable biomass, especially of cultivated millet, to be esti-

mated at an early stage in plant development. Many of these studies (Bartolomé, 1988; Rasmussen, 1992) have employed the Normalized Difference Vegetation Index (NDVI) as a proxy for the absorbed radiation and by regression analysis linked it to the observed yield. Detailed ground-based radiation studies (e.g. Bégué et al., 1991) have made it possible to estimate yield production based on absorbed radiation. In connection with large-scale field experiments (e.g. the HAPEX-Sahel, Goutorpe et al., 1997) and the development of the eddy covariance technique, our general knowledge on the functioning of the Sahelian ecosystems, manipulated as well as natural, has recently been greatly improved (Levy et al., 1997; Hanan et al., 1998; Boegh et al., 1999A).

The aim of the present project is to examine to what extent the above-mentioned improved modelling of the

photosynthetic processes can be implemented and adjusted for the conditions in northern Burkina Faso. By applying such a model it would then be possible to examine some of the limiting factors affecting crop growth (e.g. radiation, soil water availability or temperature). A comparison of yield estimates must consider the question of scale and thus the heterogeneity of the Sahelian landscape. When monitoring the conditions for plant growth at the village/landscape scale, methods which are adoptable to and can be expanded by the use of satellite data are clearly preferable. In order to focus on the objectives of the present study, the main emphasis will be placed on estimating the production of the most important crop in the Sahel, namely millet. The study includes the following steps:

- a) Long-term monitoring of carbon dioxide exchange above a millet stand in the Dori/Petakole area in the Séno province of Burkina Faso
- b) Elaboration of a photosynthesis model that incorporates physical and biochemical factors affecting plant growth in the Sahel, and a comparison of measured and modelled carbon assimilation with yield estimates obtained by interviews with the local farmers.
- c) Analysing the dependence of carbon assimilation on radiation, temperature and soil moisture through a sensitivity study using the elaborated photosynthesis model.

Methods

The experimental work was carried out near the village of Petakole (14°01' N, 0°03'E) which is located 5 km SE of Dori in the Séno province of northeastern Burkina Faso. The data set consists of two sets of micro-meteorological observations collected during the peak growing season. In 1996, the measurement period lasted from Day 240 to Day 280, and in 1997 from Day 242 to Day 277. In both years, the same millet species (*Pennisetum gambiense*) was sown and the instrumentation was mounted approximately in the middle of a 4.8 ha cultivated field. Except for patches of sorghum covering less than 15% of the area, the neighbouring fields, however, were also sown with millet allowing fetches in all directions to more than 500 m.

The soil type of the millet field is sandy soil originating from ancient aeolian deposits. The soil is low in both carbon (0.2%) and nitrogen (0.04%) content, manure is ap-

plied but at a lower level than the village average. The field is flat and the main physical obstacle consists of 3-4 acacia trees growing near the boundary of the field. Whereas germination and growth of the millet were successful in 1997, the 1996 crop suffered from a dry spell early in the season which caused whitening of the young shoots and re-sowing was not undertaken until the last week of July. Consequently, the two crops developed rather differently; in 1996 the maximum Leaf Area Index (LAI) was only 0.4 whereas in 1997 it was 0.7.

Canopy development, biomass and grain yield

Leaf Area Index (LAI) was estimated approximately every week by measuring the transmission of diffuse light through the canopy with an optical sensor (LAI-2000 Plant Canopy Analyzer, LI-COR Inc., Nebraska, USA). A porometer (AP4, Delta-T devices, Cambridge, UK) was used for manual measurement of stomatal resistance on 75 leaves. Based on the porometer data and visual inspection the leaves were divided in two categories green leaves and non-functioning senescent leaves. The Green Leaf Area Index (GLAI) was then calculated as LAI times the ratio of the number of green leaves to the total number of leaves. Within an area of 100 m by 100 m surrounding the mast both plant height and LAI were measured in 25 regularly spaced grid cells. For the 1996 growing season, the total above-ground biomass was estimated by harvesting and weighing all the millet plants within the 25 grid cells each measuring 20 m by 20 m.

Harvest data were obtained by interviewing 39 farmers who cultivated a total of 85 village fields with millet. The recall period was 3 months for the 1997 and 1996 harvest, and 15 months for the 1995 harvest. Millet is harvested in bundles and counted in such by the farmers. All farmers could recall the size of their total harvest at least two years back, while some could only remember field specific yields one year back. The aggregated harvest of village fields was calculated on the basis of average bundle weights times the number of harvested bundles for each farmer. The size of each field was measured by a trained assistant using 'the steps and compass' method. The size of the total cultivated area was measured by use of a GPS, and controlled by aerial photographs.

For converting the CO₂-fluxes into yield, it is used that it takes 2.1 g of CO₂ to produce 1 g of dry matter (Penning de Vries et al., 1989). To be able to separate between above-ground biomass and total biomass, the ratio between

shoots and roots was studied during the HAPEX-Sahel (Hanan et al., 1997) by sieving the soil samples taken around two millet clumps down to a depth of 2 m. It was found that the weight of the roots was 328 g while the above-ground biomass was weighted to 642 g, giving a shoot:root ratio of 2:1. For converting above-ground biomass into yield estimates a harvest index (HI) of 0.2 was used (Bégué et al., 1991).

Measurement of CO₂ fluxes and meteorological data

The fluxes of carbon dioxide and water vapour above the vegetation were measured using the eddy covariance technique (Baldocchi et al., 1988). The measuring mast was equipped with a 3-D sonic anemometer (Gill Solent, UK). An IRGA (InfraRed Gas Analyzer, LI-COR 6262, LI-COR Inc., USA) with a built-in sensor for pressure corrections was used for measuring carbon dioxide and water vapour concentrations. Due to the heterogenous growth of the millet in 1996, the sonic anemometer and the inlet to the IRGA sampling tube were raised from 3 m to 6 m above ground level in the middle of the campaign. The sampling tube (Bev-A-Line, LI-COR Inc., USA) was 15 m in length with an inner diameter of 3.2 mm, and the air was sucked through the sampling tube by a membrane pump at a flow rate of 6 l min⁻¹. Due to an unfortunate malfunction of the pump, the CO₂-flux data from 1996 proved unreliable. In 1997 the same setup was used, with a constant measuring height of 6 m. More than 768 hours of flux data were collected. Data acquiring and processing were based on the EdiSol software package (Moncrieff et al., 1997). The flux mast was also equipped with sensors for the measurements of basic micro-meteorological parameters including; net radiation (Q*6, REBS inc., USA), soil heat flux (HFT-3, REBS inc., USA), short wave radiation (CM-7, Kipp & Zonen, NL), soil and air temperatures (thermocouple), and IR surface/ canopy temperature (KT-17, Heimann, D). Incident and reflected photosynthetically active radiation (PAR) were measured by quantum sensors (LI-190, LI-COR Inc., USA) while soil moisture was recorded by ThetaProbes which responds to the dielectrical properties of the soil (Delta-T devices, UK). Supplementary meteorological data (rainfall and temperature) were provided by L'Institut de Météorologie de Burkina Faso which operates a meteorological station in Dori. Intercepted rainfall during the growing season was calculated according to Casenave & Valentin (1989) where superficial runoff is assumed when the rainfall rate is more than 25 mm/d for

dry soil or 10 mm/d for wet soils. The infiltration capacity for the excessive rainfall is equal to 67%. The onset of the rainy season is defined as the date for the first major rainfall (>25 mm) which is not followed by dry spells lasting for more than 10 days. The end of the rainy season is the date for the last rainfall event larger than 5 mm.

Carbon dioxide model

The applied photosynthesis model is based on the "big leaf" concept (Farquhar et al., 1980), elaborated by Collatz et al. (1992) for use on C₄-species. The general idea is that the net photosynthetic rate (A_n) is calculated as the minimum of three potential photosynthetic rates (J_E , J_C , J_S) less the dark respiration. J_E is the rate controlled by absorbed PAR, J_C is the rate controlled by the stomata, and J_S is the rate controlled by removal of assimilates. Each of the limitations is scaled from leaf level to the actual canopy level (with Leaf Area Index=L) using the area of sunlit leaves per unit ground $\Pi = (1 - e^{-kL})/k$ where k is the average extinction coefficient (=0.7). The three specific equations are as follows:

$$\left. \begin{aligned} J_E &= \Pi \cdot a \cdot \alpha \cdot Q_p \\ J_C &= \Pi \cdot k_s \cdot p_i / P \\ J_S &= \Pi \cdot V_m \end{aligned} \right\} [\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}] \quad (1)$$

where a is the leaf absorptance of PAR (0.86), α is the initial slope of the light response curve, Q_p is the photosynthetic active radiation ($\mu\text{mol m}^{-2} \text{ s}^{-1}$), p_i is the intercellular CO₂ partial pressure (Pa), k_s is the initial slope of the photosynthetic response to p_i , and P is the air pressure (Pa). The photosynthetic rate is related to the Rubisco capacity, V_m (i.e. the catalytic capacity of Rubisco, the CO₂ fixing enzyme). Because V_m is temperature dependent ($Q_{10}=2$), it is for reference scaled to a common temperature 25 °C and denoted V_{m25} . The net assimilation is then calculated by:

$$A_n = \min(J_E, J_C, J_S) - R_{ul}L \quad [\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}] \quad (2)$$

Eqn. 2 indicates a sharp transition from one limitation to another. However, when two or more limitations are nearly equal co-limitation occur and the result, which is

slightly lower, is found by solving a quadratic function as described by Campbell & Norman (1998).

The dark respiration R_{ld} per leaf area is calculated as $0.02V_m$ (Collatz et al., 1992). The bulk stomatal resistance (r_s) in ($s\ m^2\ mol^{-1}$) is calculated by use of the Ball & Berry model (Collatz et al., 1992):

$$\frac{1}{r_s} = m \frac{A_n h_s f_w}{c_s} + bL \quad [mol\ m^{-2}\ s^{-1}] \quad (3)$$

where b ($mol\ m^{-2}\ s^{-1}$) and m are empirical constants (Table 1), h_s is the relative air humidity at the surface of the leaf (%), c_s is the mole fraction of CO_2 at the surface of the leaf, and f_w is the effect of limited soil water content (θ_s) on stomatal resistance. It is scaled using maximum (θ_{max}) and minimum (θ_{min}) soil water content (vol %) at a depth of 5 cm applying the following empirical function (Wang & Leuning, 1998) :

$$f_w = \min\left(1.0, \frac{10(\theta_s - \theta_{min})}{3(\theta_{max} - \theta_{min})}\right) \quad (4)$$

A listing of model parameters is given in Table 1. Due to the feedback coupling between A_n and $1/r_s$, the Eqns. 1-4 are solved through iteration. The photosynthesis model was designed to use a single boundary layer resistance to control the exchange above the leaf. In the present canopy version, micro-meteorological measurements at reference height are used as input parameters and the single boundary layer resistance is substituted by the sum of the atmospheric resistance and the boundary layer resistance. According to Monteith & Unsworth (1990), the atmospheric resistance (r_a) is calculated from wind speed (u) and frictional velocity (u_*), see Eqn. 5.

$$r_a = \frac{u}{u_*^2} \quad [sm^{-1}] \quad (5)$$

In accordance with Boegh et al. (1999A) the boundary layer resistance for water vapour is found as the minimum of the two resistances calculated assuming respectively molecular diffusion in laminar forced convection (Jones, 1992) and free convection (Brenner & Jarvis, 1995). Due to the larger molecules the resistances for carbon dioxide is found by multiplying by 1.4 (Jones, 1992):

$$r_{a(forced)} = 151 \sqrt{\frac{w}{u}} \quad [sm^{-1}]$$

$$r_{a(free)} = 0.93 \sqrt{\frac{w v}{D_h^3 g a_i (T_l - T_a)}} \quad [sm^{-1}] \quad (6)$$

where w is the width of leaves (0.05 m), u is the wind speed ($m\ s^{-1}$), v is kinematic viscosity, a_i is the coefficient of thermal expansion, g is the gravity acceleration, D_h is the thermal diffusivity, and $(T_l - T_a)$ is the difference between leaf and air temperature.

Calculation of canopy flux and net ecosystem flux

In accordance with Ruimy et al. (1995), the eddy covariance CO_2 -fluxes measured above the canopy during day-time (06:00-18:00) are denoted by F_d . The eddy covariance flux for the remaining 12 hours (night-time) is denoted by F_n . The sign convention used here for the carbon dioxide fluxes originates from ecophysiology, in which a flux of carbon dioxide from the atmosphere to the canopy is defined as positive, whereas an upward flux is negative. This

Parameter	Symbol	Unit	Equation	Value	Reference
Rubisco capacity	V_{m25}	$\mu mol\ m^{-2}\ s^{-1}$	below 1	39	Boegh et al., 1999A
Respiration ratio	R_{ld}/V_m	-	below 2	0.02	Collatz et al., 1992
Temp. dependence	Q_{10}	-	below 1	2	Collatz et al., 1992
Stomata model slope	m	-	3	3.63	Boegh et al., 1999A
Stomata model intercept	b	$mol\ m^{-2}\ s^{-1}$	3	0.09	Boegh et al., 1999A
Quantum yield	α	-	1	0.037	

Table 1: Model parameters for the photosynthesis C_4 -model

means, that during daytime, the net assimilation (A_n) can be set equal to the canopy flux (F_c) (Ruimy et al., 1995) defined as:

$$A_n = F_c = F_d - F_s \quad (7)$$

where the soil respiration (F_s) is directed upward and is thus negative. By definition F_s consists of heterotrophic microbial decomposition, and root respiration, but no separation of these two components is made here (see also Lloyd & Taylor, 1994). The temperature dependence of F_s is expressed using an exponential function adopted from Lloyd & Taylor (1994). Previous studies from the Sahel (Friborg et al., 1997) have shown that soil respiration also depends on the soil moisture content, and to take this into account the ratio between actual soil moisture θ_a and the soil moisture at field capacity θ_{FC} at a depth of 5 cm has been included, leading to the following equation:

$$F_s = \frac{\theta_a}{\theta_{FC}} R_{10} e^{308.56 \left(\frac{1}{56.02} - \frac{1}{T_{soil} - 227.15} \right)} \quad [\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}] \quad (8)$$

where R_{10} is the soil respiration at 10 °C and T_{soil} is the soil temperature in the upper 5 cm. As will be discussed later R_{10} can be estimated from nocturnal fluxes. The night-time eddy covariance flux (F_n) originates from soil respiration, and dark respiration from the plants as defined by:

$$F_n = F_s - R_{td}L \quad (9)$$

The dark respiration is included in the A_n -term, and during nighttime when the rate of photosynthesis is nil $R_{td}L$ is equal to $-A_n$ (Eqn. 2).

Results

CO₂ fluxes day and night

Figure 1A and 1B show two examples (Day 262 and Day 275) of the daytime courses in the CO_2 fluxes both measured and modelled. The three individual limitations (J_E , J_C and J_S) are also included on the graphs. By adopting the parameters obtained from a similar study in Niger (Boegh et al., 1999A) (Table 1), it is possible to simulate F_c with reasonable accuracy both at the middle and at end of

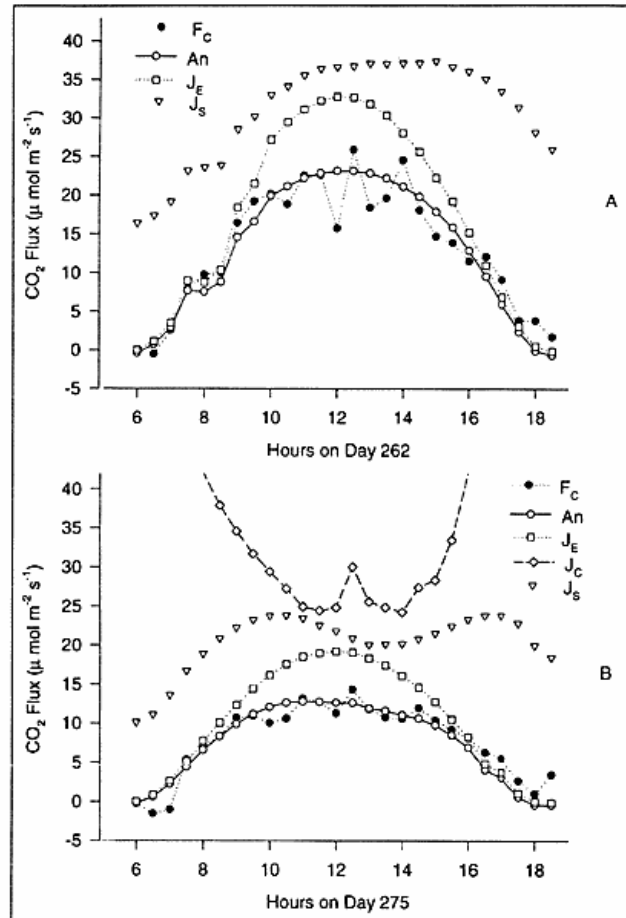


Figure 1: Diurnal variation in measured CO_2 flux (F_c) and net carbon assimilation (A_n) modelled by use of the photosynthesis model. Also shown are the major limitations (J_E , J_C and J_S) A) Day 262 (19 September, 1997) the limitation (J_C) is above $40 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and does not appear in the graph. B) Day 275 (2 October, 1997).

the growing season. On Day 262 the two controlling limitations are light (J_E) and removal of assimilates (J_S) whereas stomatal control does not cause any limitation in the CO_2 assimilation because J_C is above $40 \mu\text{mol m}^{-2} \text{ s}^{-1}$ all day. On Day 275, when the soil is drying out and the air humidity has become low, limitations in carbon assimilation due to increased stomatal resistance become important (J_C). The shape of the A_n -curve is also influenced by inhibitions as the leaf temperatures above $40 \text{ }^\circ\text{C}$ cause an afternoon secondary minimum in J_S . The implications of a low stomatal control (i.e. the relatively high J_C values) have previously been reported (Levy et al., 1997; Boegh et al., 1999A), and this aspect will be discussed later.

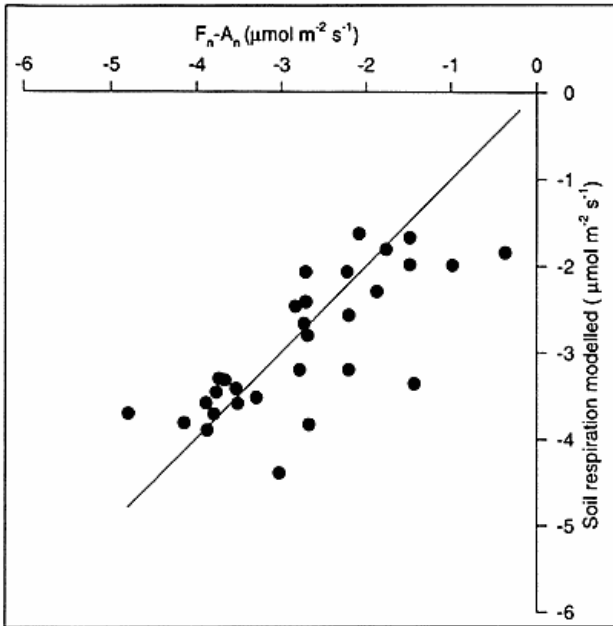


Figure 2: Comparison of soil respiration derived as nocturnal fluxes corrected for leaf respiration on the X-axis and by use of Eqn. 8 (Y-axis).

Figure 2 shows the calibration of the soil respiration model based on nocturnal fluxes. For each night, the mean flux (F_n) is calculated. Soil respiration (F_s) is also calculated by subtracting plant respiration as predicted by the photosynthesis model according to Eqn. 9. It was found that neither soil temperature nor soil moisture used as sole

parameters could be used in predicting the soil respiration flux. However, when using the two-parameter model (Eqn.8), the accuracy was greatly improved. The y-axis shows the model estimate using reference respiration (R_{10}) equal to $-0.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ and a soil moisture content at field capacity set equal to the maximum measured value of 17 vol. %. The x-axis shows the nocturnal fluxes corrected for leaf respiration.

As found in a number of other studies (e.g. Soegaard & Thorgeirsson, 1998), there is a considerable scatter of data points when modelling nocturnal fluxes, but since 22 out of the 29 points deviate less than $0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$, the model was consequently accepted.

By combining the photosynthesis model with the soil respiration model, according to Eqn. 7 and 9, it is now possible to simulate the CO_2 exchange above the canopy and calculate the net ecosystem production which is equal to the time-integrated eddy covariance measurements. The level of agreement between these two estimates is shown in Figure 3 for both the growing phase (until Day 267) and the senescence phase (the rest of the period). The temporal flux variation is closely associated with the Green Leaf Area Index (GLAI) both having a maximum around day 260 and then declining towards the end. As can be seen, the combined model simulates the flux measurements reasonably well. Most of the anomalies occur during nighttime when inversions occur and the wind speed is very low, causing larger fluctuations around the "true value" compared to the daytime when turbulence is much more

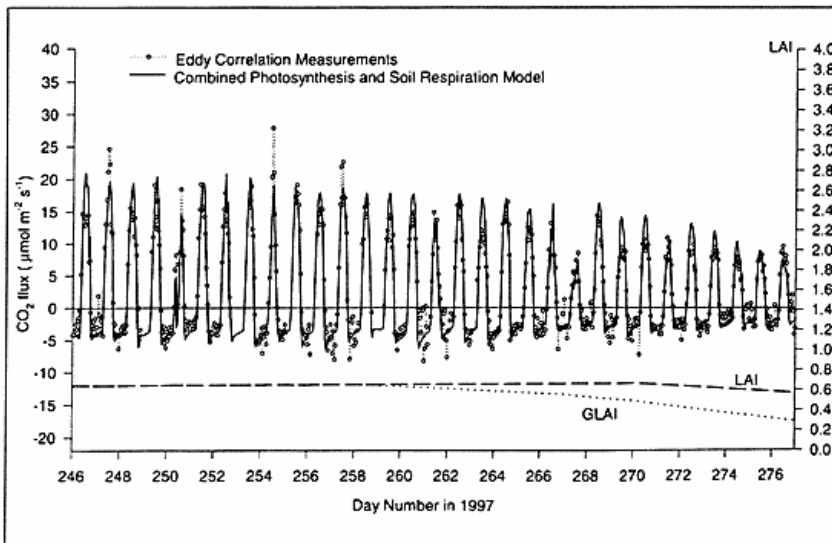


Figure 3: Temporal variation in CO_2 exchange above the millet canopy based on eddy covariance and modelling based on the combined photosynthesis model and soil respiration model. In the lower part is shown the temporal variation in Leaf Area Index (LAI) and green LAI (GLAI).

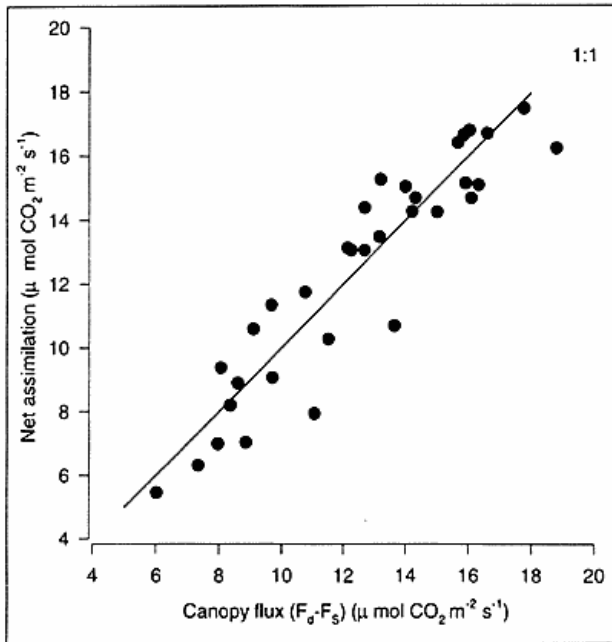


Figure 4: Net CO₂ assimilation calculated by use of the photosynthesis model plotted against canopy flux derived from eddy covariance measurements and soil respiration (Eqn. 8). Average daytime observation (6:00-18:00 h). Each point represents one day of observations. $R^2=0.86$.

developed. For the senescence phase, it is obvious that the daytime fluxes are much lower, and the diurnal variation is characterized by its midday upper ceiling, as imposed by the combined action of the J_c and the J_s limitations (confer Figure 1B).

Figure 4 compares the daytime average CO₂ assimilation as calculated by the photosynthesis model and the canopy flux calculated by Eqn. 7 for all days from Day 245 to Day 277. On days with missing half-hourly observations (see Figure 3) the daily values are found as the simple average of the actual observations. The agreement between model and observations is satisfactory as all model parameters are predefined and the slope is close to the 1:1-line with $R^2 = 0.86$. To examine the change in the CO₂ function at the time of senescence, the temporal variation in soil moisture and air and leaf temperatures are shown in Figure 5 together with measured and modelled stomatal resistance. As long as the soil is moist, the evapotranspiration will cause both leaf and air temperatures to remain low (i.e. below 35°C), but as the soil dries out, leaf temperatures exceed 40°C inhibiting plant functions and causing increased leaf senescence (Figure 3). The measured and modelled midday

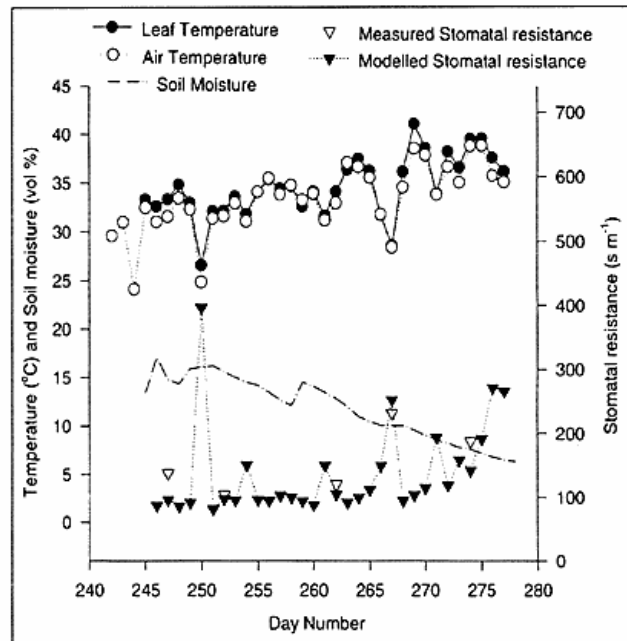


Figure 5: Temporal variation in soil moisture in a depth of 5 cm, leaf temperature and air temperature and modelled and measured stomatal resistance at noon. Petakole 1997.

stomatal resistance (r_{st}) show the same trend; for sunny days in the growing phase r_{st} is around 80 $s m^{-1}$ and roughly twice as high during senescence. This rather stepwise change in r_{st} is in agreement with Soegaard & Boegh (1995). For the modelled data (Eqn. 3) r_{st} is calculated from bulk stomatal resistance r_s as $r_{st} = 1.6 \cdot GLAI \cdot r_s$, where the factor 1.6 takes account for stomata on both sides of millet leaves (Boegh et al., 1999A). The versatility of Eqn. 3 is confirmed when the modelled stomatal resistance is compared with those measured by porometry.

Different approaches have been used when modelling the lower photosynthetic activity during the senescence phase. In a study of natural vegetation in Niger Hanan et al. (1997) used a decrease in rubisco capacity to account for lower CO₂ assimilation at the end of the season. Measurements of leaf nitrogen during the 1997-campaign show, however, a nearly constant nitrogen content (2-2.5%) which does not support the hypothesis concerning decreasing Rubisco capacity. In general it is likely that several physiological features alter more and less simultaneously when the senescence occurs, as argued by Boegh et al. (1999A).

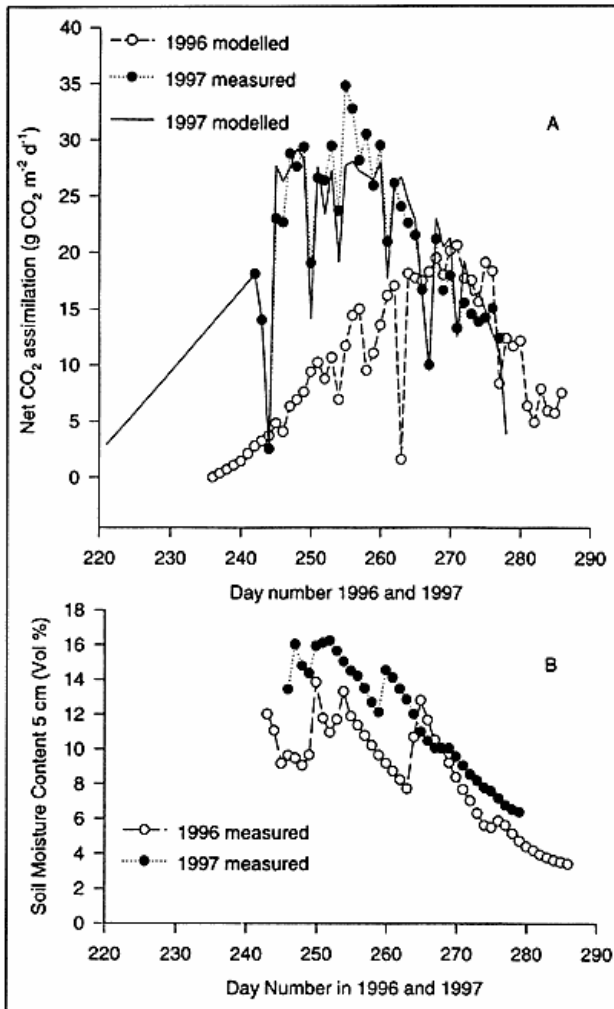


Figure 6: Net CO₂ assimilation calculated by use of the photosynthesis model for 1996 and from eddy covariance CO₂ measurements less soil respiration for 1997. Prior to Day 242, the 1997 graph is found by linear interpolation.

Comparing carbon assimilation from subsequent years

Employing the photosynthesis model in the form elaborated on the basis of data from Niger (Boegh et al., 1999A) and verified in Figure 4, it is now possible to simulate the seasonal course in carbon assimilation in 1996 and compare it to the measurements and modelling from 1997. The results of the calculations are shown in Figure 6A and reveal a large difference in the assimilation between the two years. The growing season in 1997 already starts around Day 220 and attains a daily assimilation rate of 15 g CO₂ m⁻² d⁻¹ on Day 242 increasing to 35 g CO₂ m⁻² d⁻¹ by Day 255. Thereafter there is a rapid decrease until the end

of the campaign (Day 278). By comparison hereto the 1996 growing season simulation is different in both timing and magnitude. When comparing Figure 6 A and Figure 6 B the difference in carbon assimilation between the two years seems to be associated with the development in soil moisture. In fact there is a number of environmental conditions which changes more or less simultaneously with the drying of the soil. The lower soil moisture content will thus cause an increase in bulk stomatal conductance (Eqn. 4) which for millet may result in a reduction green LAI and at the same time cause leaf temperatures to increase. In Figure 6 B it is shown that until day 265 the soil moisture content in 5 cm is one-third lower in 1996 than in 1997. In 1996, the canopy develops much later and reaches a maximum of 20 g CO₂ m⁻² d⁻¹ only at the end of September (Day 272) when the soil moisture integrated over the upper 50 cm is still above 10 vol. %.

Comparing yield estimates from interviews and carbon dioxide fluxes

The grain yield estimates are shown in Table 2 based on two different methods; i) the photosynthesis modelling and ii) local interviews with the farmers. The total CO₂ assimilation is converted into total dry-matter (dm), above-ground dm and finally yield by applying the set of conversion factors presented in the method section. From the interviews the number of millet bundles was counted to be 2195 in 1996, and 4283 in 1997, for the whole village, comprising 120 ha of fields. The average grain content of one bundle was found to differ from one year to the next. The average grain content of 47 bundles in 1996 was 12.1 kg, but as high as 18.1 kg (n=40) in 1997. The grain content per bundle for 1995 was calculated by averaging the 1996 and 1997 estimates.

Using these figures the millet grain yield pr m² is calculated and the results are presented in Table 2. The table shows that the two totally independent methods give results which are of the same magnitude. The difference in 1996 is thus 7 g m⁻². In 1997, the harvest result is 15 g m⁻² higher than that reached by the photosynthesis model. This larger discrepancy is properly due to fertilization. In dry years (1996) the low degree of fertilization applied to the study field (relative to the surrounding fields) is less important because the millet production is mostly controlled by water availability, whereas in wet years millet production benefits from a higher level of fertilization, and the yield from the study field is probably less than on the more

Table 2: Grain yield based on photosynthesis modelling and farmer interviews.

Parameter	Unit	1995	1996	1997
Eddy covariance measurements				
CO ₂ assimilation	g m ⁻²		524.0	942.4
Dry matter production	g m ⁻²		249.5	448.7
Above ground dry matter	g m ⁻²		166.4	299.2
0.2*above ground dry matter	g m ⁻²		33.3	59.8
Farmer interviews whole village				
Bundles		3095	2195	4283
Bundle weight	kg/bundle	15.3	12.6	18.1
Total yield	kg	47353	27657	77522
%millet of whole area		85.5	87.0	85.0
Millet area	ha	88.1	104.6	102.9
Grain yield	g m ⁻²	53.7	26.4	75.3
Rainfall data from Dori				
Intercepted rainfall (growing season)	mm	292.8	205.5	354.1
Length of rainy season	days	69	69	90

fertilized surrounding fields. In 1996, further comparison can be done because the above-ground biomass was weighed for each of the 25 (20 m by 20 m) grid cells surrounding the mast. The harvesting results give 151 g m⁻² ± 52 g m⁻²; which is quite close to the 166 g m⁻² above-ground dry matter reported in Table 2. In this comparison it is assumed that the water content (10-15 vol.%), at harvest time is more or less counterbalanced by the remaining biomass not collected during the harvest. In Table 2 yield data is also shown for 1995 together with intercepted rainfall and the length of the rainy season, and there are obvious differences among the three years. In 1997 the rainfall was equally distributed over a 90-days period which should be optimal for the millet variety grown in the region. In both 1995 and 1996 dry spells around Day 200 (late part of July) shortened the length of the coherent rainy season to less than 70 days. The amount of inter-

cepted rainfall was only 82% and 58% of the 1997-value, respectively in the two years.

Dependence of carbon assimilation on environmental conditions

By use of the photosynthesis model it is possible to examine the influence of changing environmental conditions on the carbon assimilation of the millet crop.

Already from Figure 1A and 1B it was shown that during the wet part of the growing season the major limitations for carbon assimilation were radiation and the removal of the assimilates largely controlled by the rubisco capacity and the leaf temperature. In the last part of the growing season the stomata control becomes increasingly important (Figure 1B) especially when the soil is drying out as shown in Figure 5.

In Table 3 the major results of simulation are given for three important environmental properties namely photosynthetic active radiation (PAR), soil moisture and midday leaf temperature. In the simulation average weather and soil moisture data from Day 269 to Day 277 have been used. Severe water stress is assumed to result in withering of the leaves and thus reduction of GLAI rather than increased stomatal resistance (confer Figure 5). The response factor is defined as the percentage change in daily assimilation divided by the percentage change in the specific parameter. It is assumed that for plant growth 0 °C can be considered as a "true" zero point thus allowing calculation of percentage changes from the Celsius scale. The carbon assimilation is found to respond rather linearly on any change in the amount of PAR as long as J_E is the major limitation. When the change becomes larger the response is reduced as the other limitations for plant growth (J_C and J_S) become more important.

The effect of low soil moisture content is expressed through the role of the water stress function (Eqn. 4). As long as the soil moisture content is above approximately 8

Table 3: The sensitivity of carbon assimilation with respect to changes in environmental conditions. Mean values for Day 269 - Day 277.

Environmental parameter	Photosynthetic Active Radiation Daily totals	Soil moisture Daily average	Soil moisture Daily average	Midday leaf temperature	Midday leaf temperature
Nominal value	40 mmol m ⁻² d ⁻¹	2.8 Vol %	>8 Vol %	<36 °C	>36 °C
Change in value	+10 %	-50 %	-50 %	-10%	+10%
Change in assimilation	+ 6.8 %	- 45 %	- 0.5 %	-5.1%	-5.4%
Response factor	0.68	0.90	0.01	0.51	-0.54

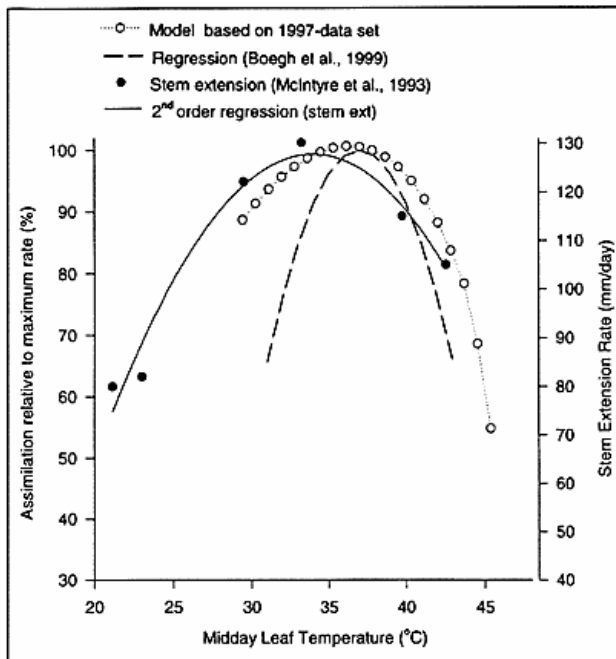


Figure 7: The plant growth rate dependence on leaf temperature.

- 1) Based on the photosynthesis model average daytime values (Day 267-Day 277, 1997)
- 2) Maximum assimilation rates calculated from light response curves by Boegh et al. (1999A)
- 3) Based on stem extension measurements by McIntyre et al. (1993).

vol. % water stress does not play any role but for lower soil moisture content the function becomes very important especially through the associated lowering of the GLAI.

The temperature dependence of carbon assimilation changes with the actual leaf temperature, and the assimilation rate decreases for both increasing and decreasing temperature as shown in Table 3 and Figure 7. For comparison with other results the data have been scaled relative to the maximum assimilation rate. The comparable results include simulations based on measurements from Niger, (Boegh et al., 1999A) where an optimal leaf temperature of around 36 °C was found. For both increasing and decreasing leaf temperature, the net CO₂ assimilation rate was found to decrease. The third plot in Figure 7 is based on a study from India (McIntyre et al., 1993) showing that during the growing phase both very high and very low air temperatures reduced the daily stem extension with respect to the maximum value of 130 mm d⁻¹. For comparison, the original daily mean air temperatures (T_m) are converted to daytime leaf temperatures (T_l) by use of linear regression:

$T_l = 1.86 T_m - 19.3$ ($R^2 = 0.83$) derived from the Petakole data. When plotting the data from India in Figure 7, there is an encouraging agreement among all three estimates confirming that the growth rate of millet depends strongly on temperatures.

Discussion

In order to estimate net carbon assimilation in a millet stand, a mechanistic photosynthesis model elaborated by Collatz et al. (1992) and modified by Boegh et al. (1999A) has been adopted. Originally this photosynthesis model did not include limitations in the assimilation rate due to water stress. To take account of the water stress situation observed at the end of the 1997 growing season, a water stress factor proposed by Wang and Leuning (1998) has been included. This seems to be a useful step because it improves the simulation at the end of the growing season (primo October) when the moisture content in the upper part of the soil approaches 3-4%. In combination with the use of GLAI rather than LAI in the modelling it seems that the present model is effective in capturing the temporal variation in CO₂-assimilation throughout the season. For the two years with micro-meteorological measurements (1996 and 1997) the yield estimates based on interviews and those based on carbon flux measurements and photosynthesis modelling were found to be within the same magnitude ($\pm 25\%$).

The present simulation results confirm the findings by Boegh et al. (1999A) who used a similar photosynthesis model to study the net CO₂ assimilation dependence on the change in various environmental parameters. Among the meteorological parameters Boegh et al. (1999A) found that leaf temperature and photosynthetic radiation had the strongest influence on the millet growth rate, while other meteorological parameters such as air temperature, water vapour, and CO₂ partial pressure had only a marginal influence. In another simulation study from Niger, Agnew (1990) found that the annual rainfall had a significant contribution when predicting millet yield. From three years of data from Petakole village it was found that the millet yield increased with increasing amount of intercepted rainfall (Table 2), the data material was, however, too limited to draw any statistical conclusions.

The biomass measurements conducted within the grid surrounding the mast underlines the fact that there is con-

siderable variation in primary production within the individual millet fields. For large scale monitoring this is in favour of sampling methods which are integrating the data over larger areas (e.g. eddy correlation technique / remote sensing). For the biomass modelling it is also important that the models can be applied to larger scales. Thornton et al. (1997) have by use of their CERES model demonstrated that they are able to predict the millet production for the whole of Burkina Faso using standard weather data combined with information on land surface properties such as soil type and drainage conditions but without the use of data on vegetation density (i.e. LAI). By contrast, Boegh et al. (1999A) have shown that the amount of data necessary to run the mechanistic photosynthesis model can be limited to three parameters: LAI, midday leaf temperature, and irradiances; through which there is a natural link up to remote sensing because both LAI and leaf temperature are satellite measurable quantities (Boegh et al., 1999B; Troufleau & Soegaard, 1998; Prihodko & Goward, 1997). In Burkina Faso the use of satellite remote sensing for estimating vegetation density, not only at the landscape level but also at a regional scale, has recently been the object of a pilot study (Lind & Fensholt, this issue). It should be stressed, however, that leaf area is not solely dependent on weather conditions, but also depends on farming practices; such as soil preparation, sowing time, sowing distance between millet pockets, etc.

Consequently, when predicting plant production in the northern part of the Sahel zone, as found within the Dori area, it seems necessary to combine information on land use (including vegetation type), land management practice, vegetation density and vegetation and water status (remotely sensed). This data integration can be achieved by running the mechanistic photosynthesis model in a GIS environment; a technique previously applied in other environments (e.g. Soegaard et al., 1999).

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